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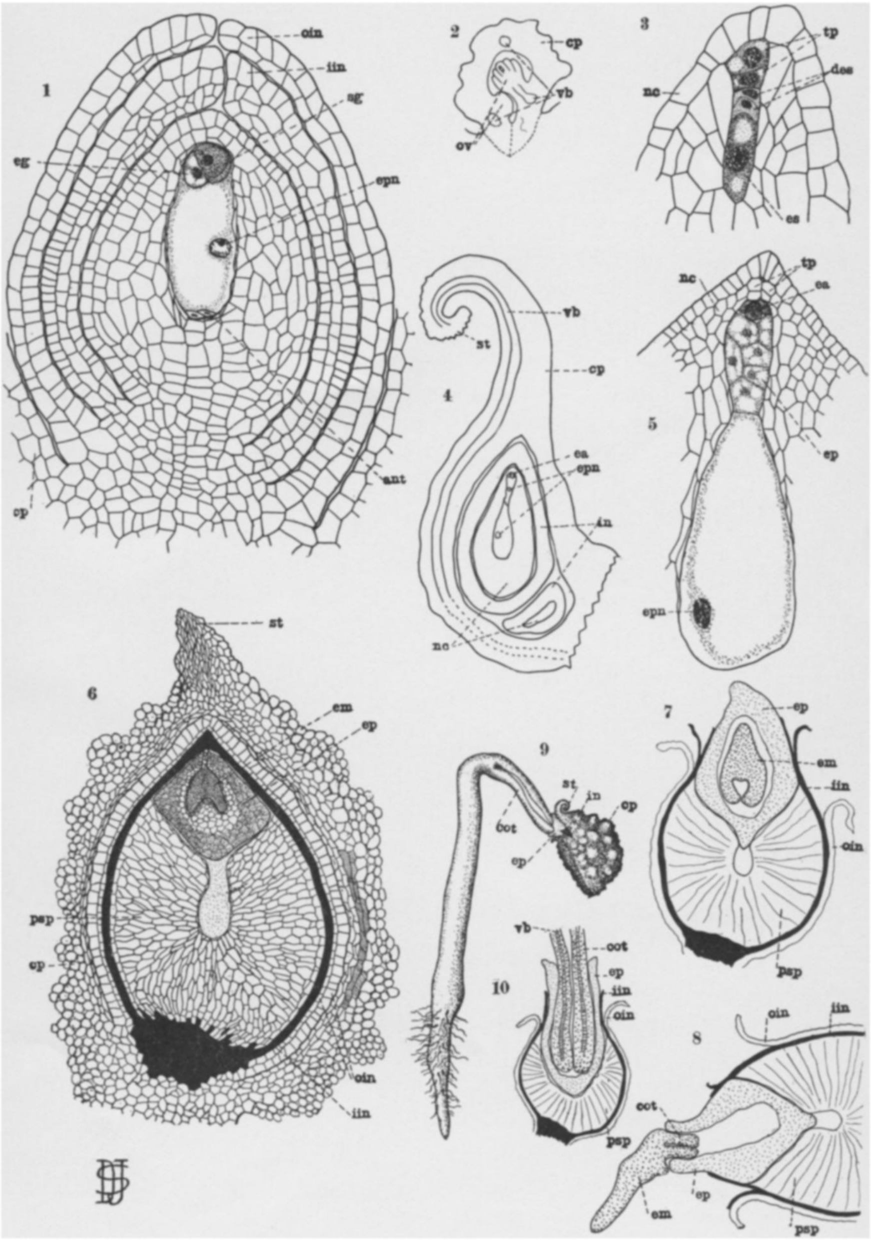

JOHNSON ON SAURURUS.

VOL. 27 No. 7

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JULY 1900

On the Development of Saururus cernuus L.

BY DUNCAN S. JOHNSON

(WITH PLATE 23)

The naked flower and the form of the carpel of *Saururus* have always led botanists to place it among the simpler Dicotyledoneae, usually in the Piperaceae. Engler has recently aroused new interest in all of these forms by separating from the Piperaceae the genera *Saururus*, *Anemiopsis*, and *Houttuynia* and constituting of them the family Saururaceae, which he regards as the simplest of the Dicotyledoneae after *Casuarina*. It was the desire to discover whether the evidence obtained from a study of the details of development would bear out this view of Engler that led me to undertake work on the Piperaceae collected by Professor Humphrey in Jamaica in 1897, and on material of *Saururus cernuus*, collected in Baltimore and North Carolina in 1899. The work on the Piperaceae will appear elsewhere and I give here a preliminary account of some features of the development of *Saururus*.

The one to three spikes of flowers are terminal in origin, but are soon pushed aside by the more vigorous growth of the last lateral bud. The flower consists of six stamens, and usually four carpels somewhat fused at the base, borne on the upper surface of a spoon-shaped bract. According to De Candolle the whole flower may sometimes be stalked from the axil of the bract.

The stamens arise on the upper and outer surface of the bract when the latter is but a slight swelling from the side of the axis. Soon after this the carpels appear as horseshoe-shaped elevations in the area within the circle of stamens, the lower flowers of the spike being always much further developed than the upper ones.

The stamen has four pollen-sacs, each with a many-celled archesporium, the wall and tapetum being formed in the usual way. The pollen grains are shed soon after the definitive macrospore of the same flower is formed. They are then binucleate and have a large thick area in the wall on one side. Nothing has been seen as yet of the sprouting of the pollen grain or the mature pollen tube. Further careful work will probably discover this, though it is certain that the pollen tube is much less prominent in the tissue of the style than in the related genus *Peperomia*.

Soon after the edges of the carpel meet and before they have fused far above the base, a single ovule appears on the inner face of each half of the carpel near the suture (*ov*, Fig. 2). These ovules are clearly lateral in origin and not, in any case seen, basal as described by De Candolle. Neither was any case found of a third or fourth ovule as described by Bentham and Hooker, though the latter character may perhaps be variable like the insertion of the flower noted above.

The ovules are sessile, orthotropous and at first transverse. They originate at about the same level, but very soon one pushes above the other with the micropylar end upward, and elongates parallel to the axis of the carpel until finally it fills practically the whole cavity of the latter. The lower ovule may develop far enough to form a ripe embryo-sac, but no case of fertilization of this was seen, and in the later stages it is transverse and flattened against the bottom of the cavity of the carpel by the erect upper ovule (*nc*, Fig. 4). The latter develops to form the single seed of the ripe fruit (Fig. 6).

The archesporial cell is single and axial, though at first there are often two or three cells equally near the axial position in the nucellus. The primary archesporial cell divides to form a tapetal cell and a definitive archesporium. The former gives rise to but few cells (*tp*, Fig. 5), which do not thicken their walls as do the tapetal cells of *Peperomia*.

The definitive archesporial cell or macrospore mother cell divides by mitosis into an upper and a lower cell, of which the upper divides once more while the lower immediately develops into the functional macrospore or embryo-sac mother cell, which pushes downward into the nucellus and upward to destroy the two degenerating macrospores above (*es*, *des*, Fig. 3).

At about the time that the primary archesporial cell becomes distinguishable the development of the inner integument begins. This is soon followed by the outer integument, arising in the same way from the surface cells at the base of the nucellus; both integuments closing in to form the micropyle at about the time the macrospore begins to encroach on its sister cells. The first division of the macrospore is transverse, and the following divisions apparently occur in the normal manner, as we find a little later an eight-nucleate and then a typical seven-nucleate embryo-sac (Fig. 1). The oosphere is rather clear or with large vacuoles, while the synergids which also have definite walls, have much denser contents (*eg*, Fig. 1). The polar nuclei fuse near the middle of the embryo-sac to form a nucleus twice the size of the egg nucleus (*epn*, Fig. 1). The antipodals are apparently quite normal at first, each with a darkly staining nucleus, but they soon become flattened against the base of the embryo-sac. Then their nuclei disorganize and the antipodals are no longer distinguishable, probably playing no further part (*ant*, Fig. 1).

After the seven-celled embryo-sac is formed it grows rapidly, especially in length, breaking down the tissue of the enlarging nucellus till it reaches two-thirds of the way to the base of the latter (Fig. 4), a length of 250 micromillimeters. Finally it broadens at the base, remaining narrow at the top, assuming thus the shape of a long-necked flask, with the egg apparatus at the top and the endosperm nucleus at the base of the neck.

It is evidently at about this time that fertilization occurs, for soon after this the endosperm nucleus divides. One of the daughter nuclei remains in the neck while the other moves down into the body of the flask, and then a wall is immediately formed across the base of the neck giving rise thus to two endosperm cells (*epn*, Fig. 4). From this time on the upper nucleus divides frequently, a cell wall forming immediately each time, and the neck of the embryo-sac thus becomes filled with a number of endosperm cells before any change is perceived in the egg or synergids (*ep*, Fig. 5). The lower of the first two endosperm nuclei grows to a very large size (*epn*, Fig. 5), but never divides further. It lies in a thin layer of cytoplasm near the wall of this large, lower endosperm cell and seems to control the advance of the latter upon the tissue of the nucellus. The nucleus persists for a long time but finally begins to show signs of degeneration and when the seed is ripe there is no distinct nucleus to be seen. Darker granules, which may be remnants of the nucleus, are sometimes seen in the otherwise faintly staining contents of this lower endosperm cell, or haustorium as it may perhaps prove to be in function (Fig. 6).

The egg begins to develop when the neck contains a dozen or more endosperm cells. The first division and several of the succeeding ones seem to be transverse. A suspensor a few cells in length is thus formed (Fig. 6), and at the lower end the embryo is developed. The latter in the ripe seed shows a pointed micropylar or root end and two slightly projecting cotyledons below with no distinct stem apex between them (Fig. 6). An axial strand of procambium is just evident at this stage.

The endosperm of the neck has by this time expanded laterally, and uses up practically all of the nucellus above and at its sides. It thus forms a double cone of tissue occupying the apex of the seed, with its lower point pushing in the upper wall of the lower endosperm cell (Fig. 6). The cells of this cap of endosperm are thin-walled, have small nuclei and are filled with a granular darkly staining substance, evidently cytoplasm. Several layers of the endosperm cells nearest the embryo are devoid of stainable contents, though their walls are still distinct, and none but those immediately in contact with the embryo have their walls compressed together. These empty cells are shown unshaded in Fig. 6.

The fate of the synergids of the embryo-sac has not thus far been determined.

The stored food material is evidently contained chiefly in the very abundant nucellar tissue or perisperm (*psp*, Fig. 6), which is closely packed with starch. This tissue is developed by the rapid growth of the basal part of the nucellus (Figs. 1, 4, 6), which finally fills nine tenths or more of the ripe seed, the cells being arranged in rows radiating out from the lower endosperm cell (Fig. 6).

The carpel at this time forms a thick, warty coat of several or many layers of outwardly rather loosely packed cells, the whole evidently serving, by means of the enclosed air, to float the fruit in the water, into which they often fall, and by which they must frequently be transported (*cp*, Fig. 6).

The inner integument is of three layers of which the inner and outer are of transversely elongated cells, the walls of which become thickened to the occlusion of the cell cavity. The cells of the middle layer remain thin-walled and are crushed between the other two (*iin*, Fig. 6—the whole thickness of this integument indicated in solid black). The outer integument is of two layers, the outer usually of larger cells, both with thin walls (*oin*, Fig. 6). These two layers appear as a whitish filmy coat over the dark inner integument when the carpel is removed from the ripe seed. At the base of the ovule a mass of chalazal cells becomes greatly thickened in the ripe seed to complete the testa in this region (Fig. 6).

THE GERMINATION OF THE SEED

The exact time and rate of sprouting under natural conditions has not been observed as yet, since the plants under observation near Baltimore failed to develop good seeds last season. Fruits obtained on the grounds of the New York Botanical Garden were kept in moist *Sphagnum* at a low temperature, from January to May, without showing any inclination to germinate. This may possibly have been due to the absence of light, though other experiments indicate that other factors were concerned. Some of the fruits were placed in damp *Sphagnum*, others in water, and still others in soil. All were given plenty of light and kept at a temperature of twenty five degrees centigrade, but none of these gave any external indication of sprouting, and sections showed that no appreciable change in the form or relation of embryo, endosperm and perisperm occurred during two months' time.

About the first of April, however, all the seeds that had been kept warm and given light and air, began to sprout freely. Then it was found that at this time the seeds that had been cool and dark also sprouted readily when given light and heat. These observations seem to show that changes occur here, not morphological, but probably of a chemical nature, such as are known to occur in many other seeds, and that these changes can take place under quite different conditions of light and temperature.

A careful study of the processes of germination shows that the first noticeable change in the seed is a swelling of the endosperm, which finally burst through the seed coats at the top and projects through the rent in these and the carpel as a white papilla (*cp*, Figs. 7, 9). This swelling enlarges the cavity occupied by the embryo in the endosperm and soon the embryo shows signs of renewed development. The root end elongates and the cotyledons grow downward and bend together at the ends (*em*, Fig. 7). Still later the root of the embryo pushes through the tip of the endosperm papilla till finally everything but the cotyledons is free. The latter remain tightly grasped by the collar-like end of the endosperm papilla, and reach at first not nearly to the bottom of the cavity in the latter (*cot*, Fig. 8).

During this time the only change in the relation of the endosperm and perisperm is that the former pushes down slightly into the large lower endosperm cell or sac (*ep*, Figs. 7, 8). As development goes on the hypocotyl elongates, pushing the root down into the soil, and the cotyledons stretch to push the stem growing point well out of the seed in one direction (*cot*, Fig. 9), while their tips push inward and thicken to force the endosperm which covers their tips like a cap, down against the tissue of the perisperm (*cot*, *ep*, *psp*, Fig. 10). The latter is gradually broken down by the encroaching endosperm, till in the later stages of germination it forms a second cap over the cotyledons outside the endosperm (*psp*, Fig. 10). After the root penetrates the substratum the hypocotyl continues to elongate and thus the whole fruit is raised into the air supported by the cotyledons (Fig. 9). The latter become broadly ovate, with only the narrow thick tip enclosed by the endosperm, and separate at the base to allow the plumule, which is now formed, to push its way out.

In the latest stages just before the fruit drops from the cotyledons the endosperm consists of a thin layer of compressed cells, without noticeable nuclei or other contents. Though the tip of the endosperm which projects out of the seed is exposed to the light, there was no indication that functional chloroplasts are ever formed.

The perisperm is either similarly flattened against the integument, or, in other cases, the cells seem to be emptied of their starchy contents while the walls retain their former shape. Whether the endosperm plays any part in the secretion of an enzyme for the digestion of the perisperm is as yet uncertain, but soon after the embryo pushes out of the seed the endosperm cells begin to lose their contents and do not appear like actively secreting cells.

The epidermal cells of the tips of the cotyledons have very dense contents and retain this character as long as they remain in the seed. On the surface of the cotyledons, at the tip, while they are still imbedded in the endosperm far from the light, and before chloroplasts are visible in the cells of this region, structures like typical stomata are formed abundantly. These stomata or stoma-like structures seem more abundant and more widely open at the very tip than elsewhere on the cotyledons. This fact suggests their possible connection with the absorption of food material. This has, however, not yet been proven.

Of the older seedling, after the empty carpel drops off, I need say here only that the first leaf from the plumule expands during the fourth or fifth week, and the second soon follows. In seedlings of seven or eight weeks the cotyledons cease growth, at a length of about four millimeters ; the two stem leaves at this time assume nearly the typical cordate form of the mature leaf.

CONCLUSION

I have elsewhere stated that I failed to find in the development of the embryo-sac of *Peperomia* any essential primitive features, and the present study of the related genus *Saururus* has failed in a similar manner, it seems to me, to indicate this plant as especially primitive. The origin of the parts of the flower and the development and structure of the mature embryo-sac are essentially as found generally in the Angiosperms. The immediate formation of cell walls in the endosperm occurs, as Hofmeister has shown, in more than twenty different families of this group. The occurrence of further cell walls in but one of the first two endosperm cells he has also shown to be a not infrequent phenomenon. Thus *Asarum*, *Nymphaea*, *Plantago*, the Campanulaceae, Labiatae, etc., resemble *Saururus* in forming cellular endosperm in only the upper of the first two endosperm cells ; while in *Catalpa*, *Acanthus*, and other forms, it is formed in the lower cell of the pair.

Again the slightly developed embryo and the small amount of endosperm in the ripe seed, are found not only in the Piperaceae, but in such distantly related forms as *Nuphar*, *Brasenia* and other

Nymphaeaceae, as well as in many parasitic genera, of various families, and much of the nucellar tissue remains also as perisperm in certain of the Chenopodiaceae, Caryophyllaceae, and in the Cannaceae among the Monocotyledoneae. All of these facts seem to me to show that *Saururus* is not among the higher Dicotyledoneae, but for the support of the view that it is among the very lowest, we must rely entirely upon a single character, namely, the absence of the floral envelopes.

Finally the behavior of the endosperm at germination is unique so far as I have been able to learn from the literature. We may best regard it perhaps as the lower member of a series of which such seeds as those of *Phaseolus* and *Cucurbita* form the other extreme. In other words, in seeds of the latter type, the endosperm completes its function of absorbing the tissue of the nucellus, and passing this on to the embryo, during the ripening of the seed, while in *Saururus* the final result is the same, but is only reached during the germination of the seed.

Explanation of Plate 23

Abbreviations used. *ant*, antipodal; *cot*, cotyledon; *cp*, carpel; *des*, degenerating embryo-sac mother cell; *ea*, egg apparatus; *eg*, oösphere; *em*, embryo; *ep*, endosperm; *epn*, endosperm nucleus; *es*, embryo-sac mother cell; *in*, integument; *iin*, inner integument; *nc*, nucellus; *oin*, outer integument; *ov*, ovule; *psp*, perisperm; *sg*, synergid; *st*, stigma; *tp*, tapetal cell; *vb*, vascular bundle.

1. Longitudinal section of ovule with mature embryo-sac, × 250.

2. Transverse section of carpel near the base, showing two ovules. The dotted lines indicate the line of fusion of the edges of the carpel figured and of this with the adjacent carpels, × 50.

3. Tip of nucellus with tapetal cells, one functional and two degenerating embryo-sac mother cells, × 775.

4. Longitudinal section of carpel showing two ovules, one with flask-shaped embryo-sac, × 50.

5. Longitudinal section of embryo-sac slightly older than the last, × 150.

6. Longitudinal section of ripe fruit, showing degree of development of embryo, endosperm, perisperm, integuments and carpel, × 40.

7. Longitudinal section of sprouting seed, showing pushing out of endosperm and renewed development of embryo, × 30.

8. Part of longitudinal section of sprouting seed, showing embryo attached by cotyledons to endosperm, × 30.

9. A twenty-day old seedling, showing relation of cotyledons, endosperm, seed coats and carpel, × 7.

10. Longitudinal section of the seed and cotyledons of such a seedling showing the encroachment of the endosperm upon the perisperm, × 14.